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POSTFIRE RECOVERY OF CHAPARRAL ALONG AN ELEVATIONAL GRADIENT IN SOUTHERN CALIFORNIA

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ABSTRACT—Recovery of chaparral after wildfires was studied at five sites along an elevational gradient from 300 to 1550 m. In January, two months after fire, shrubs at all sites had begun resprouting but no shrub seedlings were present. Shrub resprouts were more abundant at the higher elevations although by June average shrub size was smaller at the higher than at the lower elevations. Initial shrub seedling densities were much higher than often reported for southern California chaparral and was probably due to sampling early in the growing season. Estimates of seedling mortality from March to June ranged from 68% to 98% and was dependent on the species. Herbaceous vegetation was most extensively developed at the lowest elevation site. At some sites, herbaceous perennials were a major part of the cover and these species typically established early in the season, largely from resprouts. Annuals were abundant at all but the highest elevation site and non-native annaul species dominated the flora at the lowest elevation site.

Chaparral is a shrub vegetation distributed in various elevational belts throughout parts of the southwestern U.S. though it is most extensively developed in California. This west coast component is floristically distinct from chaparral in other regions (Daubenmire, 1943). Particularly noteworthy is the dominance of California chaparral by the shrub *Adenostoma fasciculatum*, chamise, (names according to Munz, 1974) and the absence of this species in the interior.

Wildfires are common in California and chaparral vegetation has a number of characteristics which have been interpreted as evolutionary responses to frequent fires. Many of the shrub species, e.g., *A. fasciculatum*, some *Arctostaphylos* (manzanita) spp. and some *Ceanothus* spp., possess specialized lignotubers which rapidly regenerate aboveground parts after fire and a number of species produce seeds which require fire for germination. Associated with the shrubs is a diverse herbaceous flora which is sparce in the mature vegetation but proliferates after fire. Some of the species, termed 'pyrophyte endemics' (Hanes, 1977), may dominate the first year after fire and then disappear for decades until the next fire.

Previous studies have provided a great deal of information on post-fire successional changes in both the shrub and herb floras (e.g., Horton and Kraebel, 1955; Hanes, 1971; Vogl and Schorr, 1972; Keeley et al., 1981; Zedler et al., 1983). Typically all aboveground plant biomass is killed by fire. In the first spring after fire annual herbs dominate. These herbs arise from previously dormant seeds in the soil and few herbs colonize burned sites from the outside. The first growing season is also the time of establishment for the vast majority of perennial species which will dominate in later years. Short-lived suffrutescent species germinate profusely but usually do not dominate sites until the third or fourth years after fire.

Certain species, e.g., *A. fasciculatum*, resprout from basal burls on burned plants or establish seedlings from soil-stored seed. Some species, e.g., *Quercus dumosa* (scrub oak) resprout but seldom establish seedlings, and other species, such as certain *Arctostaphylos* spp. and *Ceanothus* spp., are incapable of resprouting but establish abundant seedlings in the first growing season after fire.

The purpose of this study was to provide further information about the following aspects of chaparral community post-fire recovery: (i) patterns of recovery along an elevational gradient, (ii) rates of recovery beginning in winter of the first post-fire year, (iii) differences in recovery rate and elevational distribution between sprouting and seeding life history types for both herbs and shrubs.

STUDY SITES—Characteristics of the study sites are shown in Table 1. The two lower sites were in the Verdugo Hills northwest of Los Angeles (Los Angeles Co.) and the other three were on Mt. Baldy north of Pomona (site III was in Los Angeles Co., sites IV and V were in San Bernardino Co.). All sites burned in November 1980 and as is typical of California chaparral fires, all aboveground biomass was killed. Based on the size of shrub remains, it was estimated that all sites had been free of fire for at least 15 years prior to burning. Local and federal agencies helicopter seeded much of this burned area soon after the fires with annual ryegrass (*Lolium perenne* spp. *multiflorum*).

All sites have a mediterranean climate with precipitation largely absent between April and October. Annual rainfall averaged between 375 and 750 mm from the lowest to the highest elevation site. Summer temperatures are similar across this gradient; July average temperatures are 23°C and 22°C for the lowest and highest sites, respectively. However, winter temperatures are markedly different; 12°C vs 4°C for the average January temperature at the lowest and highest sites (NOAA, 1981). Soils at all sites were shallow, coarse to moderately textured, and rocky.

METHODS—All sites were first sampled in January 1981, two months after burning, and again in March and June. On each slope 20, 2 m x 4 m plots were placed contiguously in a belt running vertically down the slope from a randomly selected point. These plots were marked and returned to on each sampling date. However, due to massive increases in herbaceous and shrub seedlings at later dates, only a subset of each plot was sampled (20, 2 m x 2 m plots). Within each plot, height was measured for all plants and the ground surface covered by each individual was estimated as follows. In most instances area cover approximated a circle and thus the diameter was recorded. In other cases rectangular shapes were more appropriate and thus length and width were recorded. For all species, both herbaceous and woody, seedlings and resprouts were noted and recorded separately.

Density and total coverage were calculated as described by Cox (1980). Average coverage and height for shrub resprouts, shrub seedlings, and herbs were compared within a site with a one-way analysis of variance and Fisher's Least Significant Difference Test.

RESULTS—Figure 1 shows changes in density of herbs and shrubs at all sites through the first post-fire year. Few herbs were present in January and peak density was in March at the lower elevation sites, where most aboveground herbaceous material was dead by June, although at the higher elevations herb denisty remained high into June. Throughout this first year, herb density was many times greater than shrub density except at the highest elevation (site V). This herb flora was composed largely of annuals although at several sites herbaceous perennials and suffrutescents were common.

Shrub resprouts were present at all sites in January but no seedlings were present at that time. The resprout population present in January

TABLE 1—Physical characteristics of study sites. All sites burned in November 1980, and were sampled during the winter and spring 1981.

	Site				
	I	II	III	IV	V
Elevation (m)	300	520	1000	1370	1550
Slope Aspect	SE	N	S	NW	SW
Slope Inclination (°)	35	45	40	30	45

represented 15 to 30% of the June resprout population at the two lowest elevation sites (I & II) but < 2% at the two highest elevation sites (IV &V). In June, shrub density was greatest at the highest elevation site and resprouts comprised > 50% of the shrub density. At the lower elevation sites shrub resprouts were infrequent and shrub density decreased from March to June, largely due to seedling mortality.

Shrub seedling and resprout height and average coverage increased from January to June at all sites (Table 2). At the end of the first growing season shrub seedlings were significantly ($P < 0.05$) smaller than shrub resprouts and herbs. Along the elevational gradient, shrub seedling cover increased with elevation whereas there was a marked decrease in resprout cover and height from the lowest to the highest elevations. In addition, herbs tended to be larger than shrub resprouts at the highest elevation.

Many of the differences observed along this elevational gradient are related to site differences in species composition (Table 3). Although most slopes had 7 to 9 shrub species (expect site IV with 3) generally only 2 or 3 shrubs were common on any one slope. Differences among slopes appeared to be more closely related to elevation than to slope aspect. *Adenostoma fasciculatum* was the dominant species, both in density and coverage, at the lower elevation sites but was absent from the highest elevation sites. These higher elevation sites were dominated by *Ceanothus leucodermis* and *Eriodictyon trichocalyx*, species which were absent from the lowest elevations. Along this gradient, seedlings comprised 92% of the *Adenostoma fasciculatum* population at the lowest elevation (in June) but only 12% at the upper limits of its distribution. For *Ceanothus leucodermis*, seedlings represented 100% of its population at 1000 m, 37% at 1370 m and 19% at 1550 m.

Shrub seedlings suffered extensive mortality during the spring growing season at the lower elevations. *Adenostoma fasciculatum* seedling mortality estimates increased with elevation: 68% at site I, 81% at site II and 75% at site III. Estimated seedling mortalities for other species were also quite high. Mortality for *Salvia mellifera* ranged from 78% at site II to 91% at site I. Mortality for *Ceanothus crassifolius* was 76% and for *C. leucodermis* at site III it was 98%.

The number of herbaceous and suffrutescent species ranged from 16 to 23 at the three lowest elevation sites but only 7 to 9 at the two highest elevations. One third to one half of the herbaceous species at a site were present in January. The only species exceeding 1 m^2 coverage/ha at this time were the herbaceous perennials *Marah macrocarpus* and *Calystegia macrostegius* (site I), the introduced grasses *Bromus rigidus* and *B. tectorum*

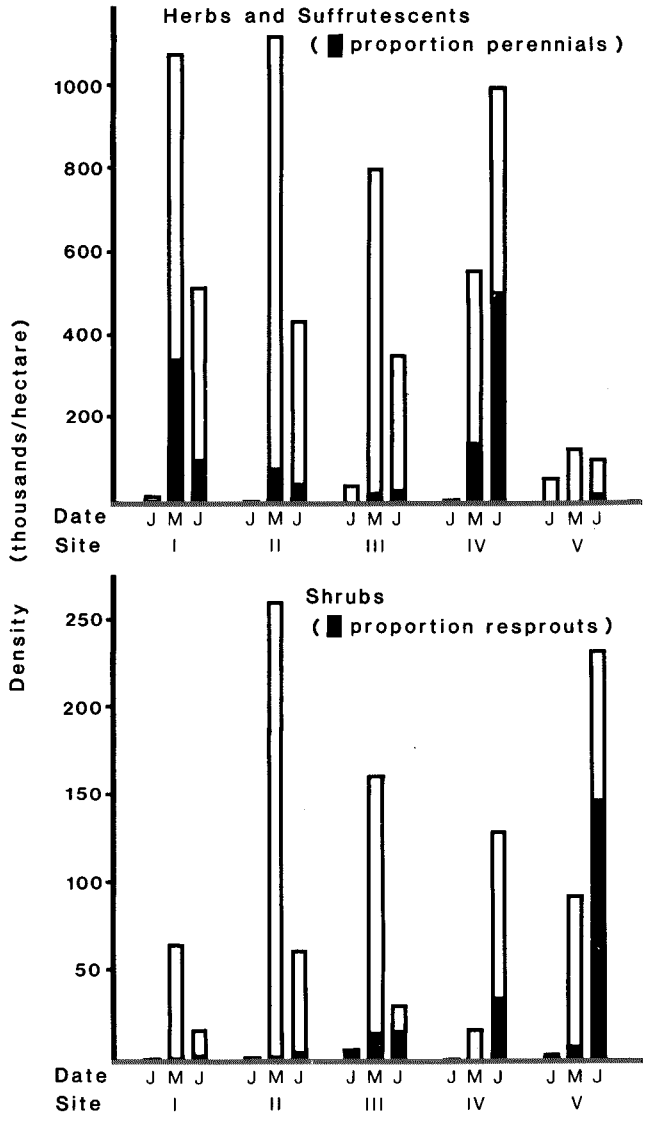

FIG. 1—Density of herbaceous, suffrutescent and shrub resprouts and seedlings in January, March, and June 1981 along the elevational gradient (I=low, V=high).

(sites III, IV, & V), and *Lolium perenne* (site V), and the native annual *Phacelia parryi* (sites I & III).

Herbaceous perennials were present only at the lowest elevation sites and established from resprouts rather than from seed. Herbaceous perennials not listed in Table 3 with > 1 m^2 coverage/ha were *Dicholostemma pulchella* (site I) and *Perezia microcephala* (site III). The suffrutescents varied in mode of establishment; *Lotus scoparius* entirely by seed, *Galium*

TABLE 2—Average height and average coverage of shrub resprouts and seedlings and herbs (including suffrutescents). All sites burned in November 1980 and were sampled during the first post-fire growing season (1981). The sites are ordered by increasing elevation. A (—) in the table indicates shrub seedlings were not present at that time.

Site		Average Coverage (cm^2/individual)			Average Height (cm)		
		January	March	June	January	March	June
I	Shrub Resprouts	86	2202	6030	11	46	96
	Shrub Seedlings	—	13	20	—	4^{a}*	14
	Herbs	9	66	599	3^{1}	$7^{a,1}$*	31
II	Shrub Resprouts	83	252	1818	7	19	64
	Shrub Seedlings	—	3	40	—	2	15
	Herbs	49	19	365	10^{1}	$4^{a,1}$	21
III	Shrub Resprouts	8	125	722	4	11	42
	Shrub Seedlings	—	3	46	—	2	14
	Herbs	4	58	240	6^{1}	3^{1}	48
IV	Shrub Resprouts	3^{a}	29	509	$2^{a,1}$	$4^{b,1}$	33
	Shrub Seedlings	—	3^{a}	37	—	2^{a}	10
	Herbs	$3^{a,1}$	$3^{a,1}$	135	$2^{a,1}$	$3^{a,b,1}$	48
V	Shrub Resprouts	3^{a}	37^{a}	329	$2^{a,1}$	$5^{a,1}$	34
	Shrub Seedlings	—	3	57	—	2	13
	Herbs	4^{a}	27^{a}	795	$5^{a,1}$	$7^{a,1}$	49

*Statistical comparison with a one-way ANOVA was made between shrub resprouts, shrub seedlings and herbs within a site on each sampling date and those with the same superscript letter are not significantly different ($P > 0.05$) with Fishers Least Significant Difference Test. At each site each growth form was also tested between sampling dates and those with the same superscript number are not significantly different ($P > 0.05$).

angustifolium and *Artemesia dracunculus* (site II) entirely by resprouts, and *Solanum xantii* (sites III, IV, and V) by both seeds and resprouts.

Introduced annual grasses and forbs were important parts of the flora at the lowest elevation site, with *Lactuca serriola* making up a large part of the miscellaneous category shown in Table 3. *Lolium perenne* (ryegrass), which had been seeded in by the Forest Service, was successful only at the highest elevation site. Native annuals were abundant at all sites though the species varied with the site; *Phacelia* species were present at most sites, *P. parryi* and *P. cicutaria* (sites I & III) and *P. brachyloba* (sites III, IV & V).

DISCUSSION—The lower elevation sites examined were on the border of the lower limits of chaparral vegetation. At these sites shrub resprouts were uncommon though the few that were present reached very large sizes by the end of the first growing season. Shrub resprouts were more important at the higher elevations and this parallels the patterns observed by Keeley and Keeley (1981) along an elevational gradient in San Diego Co. These patterns in resprouts versus seedling regeneration are seen in this study even within species; *Adenostoma fasciculatum* and *Ceanothus leucodermis* resprout/seedling ratio increased with elevation. Horton and Kraebel (1955) likewise recorded *C. leucodermis* resprouts only at their highest elevation site despite the fact that seedlings occurred at all four of their sites. Vogl and Schorr (1972) studied a high elevation site where *A. fasciculatum* resprout production was highly significant, whereas Howe (1976) found. *A. fasciculatum* resprouts to be relatively insignificant at his much lower

TABLE 3—Density and areal coverage for the dominant shrubs and herbs. All sites burned November 1980 and were sampled in the first growing season. The first sample period (January) is not included due to relatively low numbers for most species. A (−) indicates not present.

		Site I				Site II				Site III				Site IV				Site V			
		Density (10^3/ha)		Coverage (m^2/ha)		Density (10^3/ha)		Coverage (m^2/ha)		Density (10^3/ha)		Coverage (m^2/ha)		Density (10^3/ha)		Coverage (m^2/ha)		Density (10^3/ha)		Coverage (m^2/ha)	
		March	June	March	June	March	June	March	June	March	June	March	June	March	June	March	June	March	June	March	June
Shrubs:																					
Adenostoma fasciculatum	(r)†	0.2	1.0	55	115	1.7	2.5	23	538	12.2	13.2	133	1586	-	-	-	-	-	-	-	-
A. fasciculatum	(s)	37.4	12.0	73	24	73.2	14.0	26	3	47.0	1.8	14	15	-	-	-	-	-	-	-	-
Rhus laurina	(r)	0.6	1.5	138	1393	0.1	0.5	25	57	-	-	-	-	-	-	-	-	-	-	-	-
Salvia mellifera	(s)	26.9	2.5	8	5	67.0	15.0	20	80	-	-	-	-	-	-	-	-	-	-	-	-
Ceanothus crassifolius	(s)	-	-	-	-	120.0	29.0	44	97	-	-	-	-	-	-	-	-	-	-	-	-
C. leucodermis	(r)	-	-	-	-	-	-	-	-	-	-	-	-	-	2.1	-	189	-	30.0	-	1200
C. leucodermis	(s)	-	-	-	-	-	-	-	5	92.5	2.3	28	5	17.7	88.1	5	109	85.6	70.5	26	223
Salvia apiana	(r)	-	-	-	-	-	-	-	-	1.7	0.5	35	130	-	-	-	-	-	-	-	-
Eriodictyon trichocalyx	(r)	-	-	-	-	-	-	-	-	-	-	-	-	-	30.0	-	1046	5.1	108.5	19	2818
Fremontodendron californicum	(r)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	2.0	2	171
	(s)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.0	-	9
Other		<.1	<.1	<1	<1	<.1	.5	<1	38	6.6	12.2	67	87	4.5	9.0	16	132	1.6	18.5	4	586
Total		65.1	17.0	274	1537	262.0	61.5	138	818	160.0	30.0	277	1823	22.2	129.2	21	430	92.6	233.5	51	5007
Herbs and Suffrutescents:																					
Marah macrocarpus	(hp)	53.0	-	1950	-	29.0	-	1082	-	<.1	-	<1	-	-	-	-	-	-	-	-	-
Calystegia macrostegia	(hp)	204.0	52.0	440	1040	<.1	<.1	23	127	-	-	-	-	-	-	-	-	-	-	-	-
Lotus scoparius	(suf)	318.0	63.0	96	920	-	.2	-	230	-	-	-	-	-	-	-	-	-	-	-	-
Centaurea militensis	(a•)	-	57.0	-	3800					-	-	-	-	-	-	-	-	-	-	-	-
Galium angustifolium	(suf)	-	-	-	-	-	-	-	-	1.7	4.5	1	9	133.9	501.4	40	3961	-	-	-	-
Erodium cicutarium	(a•)	58.9	-	453	-	-	-	-	-	40.0	1.5	276	20	170.7	0.1	51	5	9.1	4.5	3	143
Brassica nigra	(a•)	142.0	62.0	1858	12880	-	8.0	-	188	-	-	-	-	-	-	-	-	-	-	-	-
Bromus spp.	(a•)	.1	-	22	-	20.0	6.0	24	10	159.5	90.0	688	1766	117.0	428.6	43	3386	91.1	49.4	275	1511
Lolium perenne	(a•)	2.0	-	18	-	7.0	9.0	70	16	-	-	-	-	-	-	-	-	13.9	20.0	33	1970
Phacelia spp.	(a)	113.0	42.0	1119	780	-	-	-	-	267.7	179.1	2745	4874	100.5	49.2	30	2916	-	<.1	-	1
Eucrypta chrysanthemifolia	(a)	-	-	-	-	922.0	-	1057	-	-	-	-	-	-	-	-	-	-	-	-	-
Cryptantha intermedia	(a)	-	-	-	-	47.0	138.0	17	95	72.0	29.5	266	830	3.6	5.7	1	90	0.1	9.6	1	316
Lotus strigosus	(a)	-	-	-	-	-	-	-	-	-	-	-	-	21.3	5.0	9	316	8.6	14.0	17	3789
Other		188.1	243.0	1133	20589‡	108.2	276.8	56	8134	260.3	54.4	675	1027	-	8.5	-	8	-	2.0	-	83
Total		1079.1	519.0	7089	40000	1133.2	438.0	2329	8800	801.2	359.0	4651	8526	547.0	998.5	174	10682	122.8	99.5	329	7813

†r = shrub resprout; s = seedling; a = annual; hp = herbaceous perennial; suf = suffrutescent; • = non-native.

‡A large portion of this represents plants which were dried beyond recognition.

elevation site. One species which stands as an exception to this rule is *Rhus laurina*, a low elevation vigorous sprouter which seldom establishes seedlings after fire.

The number of shrub seedlings present in March were many times greater than has been recorded in previous studies, although, the June values were comparable. For example, *Adenostoma fasciculatum* seedling densities in March ranged from 37,000 to 73,000/ha whereas June values ranged from 12,000 to 14,000/ha. The highest *A. fasciculatum* seedling density previously recorded for southern California was 14,400/ha (Keeley and Zedler, 1978). This difference may stem from the fact that previous studies have not sampled early in the growing season as was the case in the present study. Shrub seedling mortality was generally above 70% and commonly above 90% between March and June. These seedling mortalities are of the same magnitude as has been reported in recent studies (Mills, 1983; Ellis, 1983).

At sites with intense shrub seedling mortality there was an extensive herb vegetation. At these lower elevation sties herbs were more abundant and on average much larger. The fact that herbs are known to reduce shrub seedling survival (Schultz et al., 1955) may account for this pattern.

Artificial seeding of *Lolium perenne* by various agencies does not seem to have played a major role in the vegetation recovery at these sites. The purpose for seeding this species is that it establishes early in the season and may aid slope stability early in the rainy season. However, inhibitory effects of this species on the establishment of native herbs and shrub seedlings are well documented (Schultz et al., 1955; Corbett and Green, 1965; Gautier, 1981). *Lolium perenne* was abundant only at the highest elevation site. From changes in its coverage between March and June it would appear that it did more harm than good. By March it had produced little cover on the slope, however, after the rains had largely ceased, between March and June and the danger of erosion was lessened, *L. perenne* increased 60 fold in its coverage.

Other non-native annual species (not artifically seeded in) were important components at certain sites. These species, *Centaurea militensis Erodium cicutarium, Brassica nigra* and *Bromus* spp., dominated the lowest elevation site and thus it appears they are highly favored by fires at the lower elevational range of chaparral. Many of these exotic species are common in annual grasslands of California and Wells (1962) has suggested that these grasslands owe their existed to repeated fires which favor the exotic herb species over brush.

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